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Sarah Cancellieri
Portland State University

Michael T. Murphy
Portland State University, murphym@pdx.edu

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RESEARCH ARTICLE

Experimental analysis of nest-site choice and its relationship to nest success in an open-cup–nesting passerine

Sarah Cancellieri and Michael T. Murphy*

Department of Biology, Portland State University, Portland, Oregon, USA
* Corresponding author: murphym@pdx.edu

ABSTRACT
Nest placement presumably reflects selection for secure sites to minimize failure. Most tests of this hypothesis, however, have failed to support it. We used artificial nests (ARTs) to experimentally evaluate nest-site-choice behavior by an open-cup–nesting bird, the Eastern Kingbird (*Tyrannus tyrannus*). In 2010 and 2011, we placed ARTs in trees in the riparian zone at Malheur National Wildlife Refuge, Oregon, USA, to test whether (1) characteristics describing the physical location in trees of used and unused ARTs differed, (2) used ART sites more closely resembled naturally chosen sites, (3) successful natural nests (NATs) and successful ARTs were similarly located along the major axis describing nest placement, and (4) unused ARTs resembled failed NATs. Used and unused ART sites differed, but unused ART sites were more similar to NAT sites. The latter unexpected result occurred because (1) unused ARTs were located at sites between more heavily used higher and lower locations and (2) most kingbirds nesting at lower locations used ARTs instead of building their own nest. In both ARTs and NATs, differences between successful and failed nests exhibited the same pattern for most nest-site variables, and the major gradient describing nest location was the same; successful nests tended to be placed on more vertically oriented branches that were placed closer to the top of the tree. Kingbird nest placement was thus selective. However, extensive overlap in the locations in trees of failed NATs and both successful and unused ARTs suggests that other factors, such as macrohabitat characteristics or prior experience of individual birds with particular nest sites, may have influenced success and/or decisions to use or reject nests in particular locations. Thus, consideration of phenomena beyond the nest site itself may be required to fully understand the process of nest-site choice in birds.

Keywords: choice, Eastern Kingbird, experiment, nest placement, nest predation, nest success, *Tyrannus tyrannus*

Análisis experimental de selección de sitios de nidificación y su relación con el éxito del nido en un paseriforme con nidos en forma de taza

RESUMEN
Se supone que la colocación de nidos refleja selección natural para sitios seguros que minimizan el fracaso reproductivo. Sin embargo, la mayoría de las pruebas de esta hipótesis no la han apoyado. Usamos nidos artificiales (ARTs) para evaluar experimentalmente el comportamiento de selección de sitios de nidificación en *Tyrannus tyrannus*, un ave que utiliza nidos abiertos en forma de taza. En 2010 y 2011, colocamos ARTs en árboles de la zona ribereña en Malheur National Wildlife Refuge, Oregon, USA, para probar si (1) características de la ubicación física de los árboles con ARTs usados y no usados fueron diferentes, (2) sitios de ARTs usados eran más similares a sitios elegidos naturalmente, (3) nidos naturales (NATs) exitosos y ARTs exitosos se ubicaron en lugares parecidos sobre el eje mayor que describe la colocación de nidos, y (4) ARTs no utilizados se parecían a NATs fracasados. Sitios de ARTs utilizados y no utilizados fueron diferentes, pero sitios de ARTs no usados eran más similares a sitios de NATs. Este último resultado inesperado ocurrió porque (1) ARTs no usados se ubicaron en sitios intermedios entre las localizaciones más usadas altas y bajas, y (2) la mayoría de las aves anidando el lugares bajos usaron ARTs en vez de construir su propio nido. En ARTs y NATs, diferencias entre nidos exitosos y fracasados mostraron el mismo patrón para la mayoría de las variables describiendo sitios de nidificación, y el gradiente mayor que describe la ubicación de nidos fue igual; nidos exitosos solieron estar ubicados en ramas más verticales hacia la copa del árbol. Por lo tanto, la colocación de nidos por *T. tyrannus* fue selectiva. Sin embargo, el solapamiento extensivo de las ubicaciones en árboles de NATs fracasados, y ARTs exitosos y no usados sugiere que otros factores como características de macrohabitat o experiencia previa de aves individuales con sitios de nidificación particulares pudo haber influído en el éxito y/o decisiones para usar o rechazar nidos en lugares particulares. Entonces, consideración de fenómenos más allá del sitio de nidificación en sí podría ser necesaria para entender completamente el proceso de selección de sitios de nidificación en la aves.

Palabras clave: colocación de nidos, éxito del nido, experimento, predación de nidos, selección, *Tyrannus tyrannus*

INTRODUCTION

Typically, >50% of nesting attempts by open-cup–nesting passerine birds fail (e.g., Filliater et al. 1994, Murphy 2000), and ≤80% of losses are attributable to nest predators (Ricklefs 1969, Martin 1993). Concealing nests in dense cover may reduce risks of nest predation (Götmark et al. 1995, Zanette et al. 2011) by active, visually searching predators (Santisteban et al. 2002, Weidinger 2002), but dense cover is often not a reliable safeguard (Holway 1991, Howlett and Stutchbury 1996, Latif et al. 2012). Locating nests in trees well above ground is likely a better defense against ground-foraging and low-shrub-foraging predators, such as many mammals and reptiles (Burhans et al. 2002, Latif et al. 2012), as several studies have shown (Murphy 1983, Wilson and Cooper 1998, Burhans et al. 2002, Peluc et al. 2008). Nests located toward the end of branches may further reduce threats from arboreal predator species such as sciurids and some snakes, but such nests are exposed to high winds, rain, intense sunlight, and avian nest predators (Burhans et al. 2002, Latif et al. 2012). Compromises over nest location must be made, and, ultimately, it is the interplay between predator species, parental behavior, and nest location that influences site quality and probability of nest success (Murphy et al. 1997, Latif et al. 2012). Indeed, the influence of different predators on nest success likely serves as a diversifying force to help shape avian community structure through selection for use of different nest sites (Martin 1993, 1996).

Eastern Kingbirds (*Tyrannus tyrannus*; hereafter "kingbirds") breed across North America in open, savanna-like environments, in orchards, in riparian zones, and along margins of lakes and ponds (Murphy 1996a). They are socially monogamous, build their often conspicuous open-cup nests in trees (MacKenzie and Sealy 1981, Murphy et al. 1997), and have a relatively long nest cycle (Murphy 1996a) that increases the potential for detection by nest predators. Previous studies showed that kingbirds nest near the edge of the canopy at 60–70% (2–7 m) of tree height (MacKenzie and Sealy 1981, Murphy 1983, Blancher and Robertson 1985, Murphy et al. 1997). Kingbirds are known for their vigorous attacks on potential nest predators (Davis 1941, Blancher and Robertson 1982, Siderius 1993, Redmond et al. 2009a), and Murphy et al. (1997) proposed that use of nest sites high in trees and close to the canopy edge provided air space for kingbirds to initiate aerial attacks on potential nest predators (cf. Ricklefs 1977).

Habitats at Malheur National Wildlife Refuge (MNWR), where we conducted the present study, offer a different environment from previous kingbird study sites because nesting is limited almost entirely to riparian zones, and a single species, the Black-billed Magpie (*Pica hudsonia*; hereafter "magpies"), appears to be the primary cause of nest failure (M. T. Murphy personal observation). Most riparian-zone trees are young willows (*Salix* spp.) that provide few high-quality nest sites (Redmond et al. 2007). As a result, ~10% of kingbird nests at MNWR are built in preexisting conspecific or heterospecific nests from the same or, more commonly, the previous breeding season (Redmond et al. 2007, Cancellieri and Murphy 2013). Kingbirds at MNWR also nest in artificial nests placed in trees (Cancellieri and Murphy 2013). We used the latter behavior to ask whether kingbird nest-site selection at MNWR is adaptive (i.e. results in higher reproductive success). To do so, we distributed artificial nests in trees in the riparian zone to test the following hypotheses about 2 attributes: location of nest in tree and cover around nest. If nest-site selection is nonrandom and adaptive, we predicted that (1) the attributes of used and unused artificial nests would differ, (2) the attributes of used artificial nests would match those of natural nests, (3) the attributes of successful and failed natural nests would differ, (4) the attributes of failed natural nests would most closely resemble those of unused artificial nests, and (5) the pattern of difference in attributes of successful and failed artificial nests would mirror that found for natural nests. Finally, because magpies forage as family groups by methodically moving through the willows (M. T. Murphy personal observation), and the kingbird's nesting strategy appears to rely on aggressive aerial defense of relatively conspicuous nests (see above), we predicted that (6) nest success would be independent of vegetative cover around the nest and would instead be greatest for nests located either higher in the tree or closer to the canopy edge, where the powerful and maneuverable flying ability of kingbirds permit active nest defense (cf. Ricklefs 1977).

METHODS

Study Site

Malheur National Wildlife Refuge is located in southeastern Oregon, USA, at the northern end of the Great Basin Desert (42°49′N, 118°54′W). The riparian and wetland habitats created by the Donner und Blitzen River are embedded in a desert landscape rarely used by kingbirds. The refuge is ~60 km long and 3–10 km wide. Demographic and behavioral research on the MNWR kingbird population was conducted from 2002 to 2011. Our experimental work was performed mainly near Buena Vista, a site located 5 km north of the long-term main research site located in the lower third of the refuge. In 2011, we conducted additional experiments at Bridge Creek in the main research area (see map in Redmond and Murphy 2012). The refuge's gravel roads parallel the main river and its tributaries from a distance of ≤5 m and provided access to nesting habitat.

Field Methods

We used methods from previous years to conduct censuses of all nesting habitat and to document seasonal reproductive success for every kingbird pair that nested within our study areas. Every year, 2 to 4 individuals drove the roads (in 2 vehicles) and/or canoed the river over an 8- to 12-hr day to locate nests at locations where kingbirds were seen. Approximately 90% of nests were found before or during egg laying. Nests were followed closely to document dates of first-laid eggs (i.e. breeding date), clutch size, and hatching and fledging success (i.e. numbers of eggs to hatch and young to fledge, respectively). Nests were checked every other day during incubation and the nestling period. To minimize disturbance, we observed nests from a distance of 5–10 m to establish whether an adult was tending to the nest; if one was, we assumed that the nest was active and did not check nest contents. If parents were not present, we visually checked nest contents, often using a mirror attached to an extensible pole. The breeding date for nests found after egg laying was determined by hatching date or by aging young using size (Murphy 1981) and assuming a 15-day incubation period (Cancellieri and Murphy 2013). Nests were assumed to have been depredated when contents were lost completely between successive visits prior to the age when young could have possibly fledged (minimum of 14 days; Murphy 1996a). We attributed losses to weather if nests or nest contents disappeared between successive visits and the area had experienced severe weather (i.e. high winds) since the last nest check.

Artificial Nests: Construction and Deployment

Kingbirds are known to reuse nests of 4 passerines at MNWR (Redmond et al. 2007). Old nests of American Robins (*Turdus migratorius*; hereafter "robins") are reused most frequently (even more often than old kingbird nests), probably because the robin's mud nests provide a firm base for a new nest in this nest-site-limited environment (Cancellieri and Murphy 2013). We chose to model artificial nests (hereafter "ARTs") after robin nests because kingbirds recognize them as a resource and because we could more easily standardize construction of ARTs to resemble robin nests than those of any other species. To build nests, we used a plastic Rubbermaid food-storage container (12.5 cm in diameter and 8 cm deep) as a mold to form a wire frame to which a mud–grass mix was added. Twine was tied to the frame to attach ARTs to branches of trees. See Cancellieri and Murphy (2013) for a more complete description of methods and a photograph of a used ART.

Kingbirds normally arrive at MNWR by mid-May, but in 2010 we saw few before June because of unseasonably cool and wet weather. On June 2 and 3, we deployed 30 ARTs by canoe at 100-m intervals in trees at the south end of the river at Buena Vista near the Diamond Lane bridge. Ten days later, 20 more ARTs were deployed over the next 2 km of riparian habitat. Thus, 50 ARTs were available for kingbird use at intervals of 100 m along 5 km of river in 2010.

In 2011, we deployed 65 ARTs at 100-m intervals along 6.5 km of the Donner und Blitzen River at Buena Vista on May 10 and 11. This included the 5 km used in 2010 and the next 1.5 km of river. We also added 25 ARTs at 100-m intervals at Bridge Creek of the main study area on May 13 and 14 to bolster sample size. Most ARTs overhung the river at heights of 0.5 to 2.0 m above water level. Our placement of nests was constrained by the availability of usable limbs and the need to install ARTs from a canoe in a flooding river. To expand the range of sites supporting ARTs, we climbed 6 trees whose trunks were not submerged and placed 1 nest in each tree at heights ranging from 2.5 to 4.2 m above water. We also placed 10 nests near the tops (4–5 m) of trees rooted on the riverbank so that they were on the landward side of the tree.

Nest-site Characteristics

We measured nest-site characteristics (all by S.C.) only after a nest either failed or fledged young to minimize disturbance to the nesting pair and the possibility of attracting predators to nests. Six nest-placement variables were measured at natural nests (hereafter "NATs") and ARTs: (1) height of nest above ground, (2) vertical distance of nest to top (highest point) of tree, (3) horizontal distance of nest to center of tree and (4) to edge of canopy, (5) angle of main branch supporting nest, and (6) cover around nest. We intended to measure height of nest above water, but this proved impossible because of changing water levels associated with flooding in both years. Trees were rooted either on or just below the riverbank, and therefore we measured nest height as the height of the nest above the riverbank adjacent to the spot where the tree was rooted. Measurements of distance of nest to center of tree and edge of canopy were made without reference to nest branch length and instead reflected the nest's distance from the tree's geometric center and edge at that height. We used a rigid tape measure to take all linear measurements to the nearest 0.1 m, and we measured angle of the branch at the nest location using a protractor attached to a level. Angles of 0° and 90° corresponded to horizontal and vertical branches, respectively. Branches that dipped below the horizontal plane yielded negative angles. We estimated nest cover in the immediate area around the nest by recording the number of times vegetation contacted 1-cm marks of a 10-cm dowel held above and along the 4 cardinal directions around the nest. Thus, maximum potential cover was 50. Including nest dimensions (Murphy 1996a), the area over which cover

TABLE 1. Nest-placement statistics for Eastern Kingbirds at Malheur National Wildlife Refuge, Oregon, USA (2010–2011). Females either built natural nests (NAT; $n = 54$) or used artificial nests (ART) that were provided. Statistics for unused ARTs located $\leq$200 m from a nest used by Eastern Kingbirds and presumably rejected are also provided. Results of comparison of means (SE in parentheses) by analysis of variance are reported as F (P). Categories of nests that share a letter do not differ significantly. Sample sizes of used and unused ARTs were 35 and 67, respectively.

Variable	NAT	Used ART	Unused ART	F (P)
Angle of branch (°)	33.4 (5.41)A	15.5 (4.64)B	25.8 (4.06)AB	2.89 (0.059)
Nest height (m)	1.47 (0.204)A	0.47 (0.101)B	0.68 (0.116)B	11.24 (0.000)
Distance to top (m)	2.04 (0.166)A	2.91 (0.186)B	2.31 (0.117)A	6.94 (0.001)
Distance to canopy (m)	1.00 (0.066)	1.18 (0.063)	1.05 (0.057)	1.72 (0.183)
Distance to center (m)	1.60 (0.137)AB	2.12 (0.209)B	1.55 (0.106)A	3.97 (0.021)
Nest cover (%)	1.89 (0.308)A	0.77 (0.243)B	1.82 (0.286)A	3.46 (0.034)

was estimated is represented by a roughly 30 × 20 cm ellipse. A 3-m ladder was used to measure nest traits at nests that could not be reached from the canoe or riverbank.

Statistical Analysis

We included all nests in our comparison of nest success between years but restricted our analysis of success in relation to placement of nests within the riparian zone ($\leq$15 m from river). We defined "nest success" as a binary variable whereby nests either failed (i.e. no young fledged) or produced $\geq$1 young. "Fledging success" was defined as the number of young that fledged (0–4). Average inter-nest distance of kingbirds at MNWR is ~200 m (Redmond et al. 2009b) and, thus, any ART >200 m from a kingbird nest (used ART or NAT) was considered outside of a kingbird territory and was not included in the analyses. By contrast, we considered all ARTs as rejected nest sites if they were within 200 m of a NAT or used ART. Rejected ARTs were included in analyses as unused ARTs.

All variables except nest cover were approximately normally distributed. No transformation was able to correct the non-normal distribution of cover, but because it was not a major component of variation in nest placement (see below), we used untransformed values of cover. We used principal component analysis (PCA) of the 6 nest-placement variables for NATs and ARTs to produce a multivariate description of nest position in the tree and to compare successful and failed nests. We used one-way analysis of variance (ANOVA) to compare mean values of nest-placement variables and PCA axes with eigenvalues >1.0. Comparisons were made (1) among NATs and used and unused ARTs and (2) among the 4 groups defined by nest type and nest fate. Direct comparisons of placement between failed and successful NATs and failed and successful ARTs were also made using two-sample t-tests. Given that nests were (1) found for all pairs, (2) found prior to incubation for nearly all, and (3) were checked every other day, there was no need to account for differences in exposure period among nests.

To explore the relationship between fledging success and nest placement in greater detail, we examined fledging success of all used nests in relation to year, nest type, and all nest-placement variables using best-subsets regression analysis in an information-theoretic framework. The top 3 models for all combinations of 1 through 8 variables were examined. Akaike's Information Criterion, adjusted for small sample size (AIC_c), was used to evaluate model fit, with all models within 2 AIC_c units of the top model ($\Delta AIC_c = 0$) considered candidate models of potential explanatory value. Uninformative models (*sensu* Arnold 2010) were eliminated from consideration. We then calculated model weights (w_i) and judged the importance of different parameters by calculating their relative importance (Burnham and Anderson 2002) and by examining whether parameter estimates differed from zero (i.e. 85% confidence interval did not include zero; Arnold 2010). We then restricted the analyses to successful nests and tested for a relationship between number of young to fledge (1–4) and the same predictor variables used in the previous analysis. We used Statistix version 9.0 (Analytical Software, Tallahassee, Florida, USA) for all analyses and assumed $P \leq 0.05$ and $0.05 < P < 0.10$, respectively, to indicate significant and marginally significant results. Statistics are reported as means ± SE.

RESULTS

Nest-site Characteristics

NATs were placed at 37% of tree height (i.e. 63% from the top) and at 62% of the distance from the tree center to the canopy edge (Table 1). Distance of NATs from the top of the tree (~2 m) was twice the distance to the canopy edge (~1 m). Most NATs were placed on an upward-arching branch (Table 1), but nest branch angle varied widely (−70° to 90°). NATs were exposed in the immediate area around the nest because the average cover was only 4% of the maximum possible ($1.89/50 = 0.038$; range = 0 to 10 out of a possible score of 50).
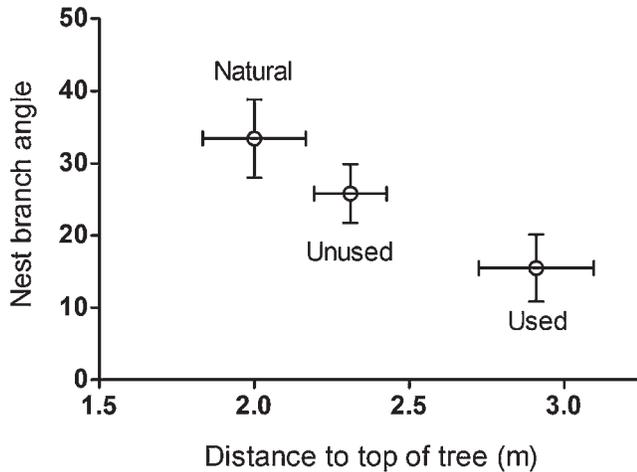
FIGURE 1. Average distance to the top of the tree and average angle of the branch on which the nest was located ($\pm$ SE) for natural Eastern Kingbird nests and unused and used artificial nests at Malheur National Wildlife Refuge, Oregon, USA (2010–2011).

The 10 ARTs placed on the landward side of trees in the riparian zone were within kingbird territories, but none were used and, thus, we did not consider them for further analysis. NATs were placed higher in trees than both used and unused ARTs, but height of used and unused ARTs did not differ (Table 1). By contrast, NATs and unused ARTs had similar distances to the top of the tree, which was less than that of used ARTs. Branches supporting NATs were marginally ($P = 0.059$) steeper than those supporting used ARTs. Overall, natural nests and unused and used ARTs were well separated with respect to distance of the nest to the top of the tree and nest branch angle (Figure 1). The position of NATs and ARTs on the horizontal plane differed little (Table 1), but used ARTs were farther from the center of the tree than unused ARTs. Nest cover of

NATS and unused ARTs were nearly identical, and significantly higher than that of used ARTs (Table 1).

Nest Success and Nest Placement
On the basis of all nests found in both years, fewer nests fledged young in 2010 (32%, $n = 69$) than in 2011 (55%, $n = 69$; 2×2 table, $\chi^2 = 6.42$, $P = 0.01$). The NATs (41%, $n = 88$) and ARTs (46%, $n = 33$) were equally likely to fledge young (2×2 table, $\chi^2 = 0.20$, $P = 0.65$). Predation accounted for 94% and 96% of all failures in 2010 and 2011, respectively. Predators were responsible for all failures of ARTs in both years and for nearly all failures of NATs in 2010 (91.9%, $n = 37$) and 2011 (93.3%, $n = 15$). Remaining losses were attributable to severe weather ($n = 2$), human activity ($n = 1$), and abandonment ($n = 1$).

Differences in nest-site characteristics between failed and successful NATs were similar to those between failed and successful ARTs (Table 2). The angle of the nest branch of successful NATs and successful ARTs was $\sim 2.35\times$ steeper than that of failed nests within respective nest types, but the difference between successful and failed nests was significant only for NATs (Table 2). Height of successful NATs exceeded that of failed ARTs, and, although not significant, successful nests of both types tended to be higher than their failed counterparts (Table 2). A direct comparison between successful and failed ARTs showed, however, that successful ARTs were located marginally higher in the nest tree ($t = 1.83$, $P = 0.08$). It follows, therefore, that successful NATs and failed ARTs were closest and farthest from the top of the tree, respectively (Table 2). On the horizontal plane, all nests were located ~ 1 m from the canopy edge, but ANOVA indicated that successful NATs were placed closer to the center of the tree than failed ARTs (Table 2). Restricting the comparison to ARTs, successful ARTs were also marginally closer to the center of the tree than failed ARTs ($t = 1.87$, $P = 0.07$). Successful NATs and ARTs thus

TABLE 2. Nest-placement statistics for failed and successful Eastern Kingbird breeding attempts that were made in either natural or artificial nests at Malheur National Wildlife Refuge, Oregon, USA (2010–2011). Means (with SE in parentheses) are compared using analysis of variance, F (P). Categories of nest type and nest success that share a letter do not differ significantly. Numbers in parentheses at column headings are sample sizes.

	Natural nests		Artificial nests		
Variable	Failed ($n = 33$)	Successful ($n = 19$)	Failed ($n = 20$)	Successful ($n = 13$)	F (P)
Angle of branch (°)	21.8 (6.76)B	51.2 (8.21)A	10.4 (5.40)B	24.8 (9.02)AB	4.97 (0.003)
Nest height (m)	1.17 (0.221)A	1.64 (0.296)A	0.34 (0.11)B	0.72 (0.196)AB	5.41 (0.002)
Distance to top (m)	2.30 (0.24)AB	1.58 (0.19)B	3.05 (0.27)A	2.74 (0.27)A	5.55 (0.002)
Distance to canopy (m)	1.02 (0.08)	0.98 (0.12)	1.12 (0.10)	1.16 (0.12)	0.72 (0.544)
Distance to center (m)	1.71 (0.19)AB	1.44 (0.21)B	2.44 (0.32)A	1.71 (0.23)AB	3.04 (0.034)
Nest cover	1.76 (0.38)AB	2.16 (0.56)A	1.20 (0.45)AB	0.15 (0.56)B	2.96 (0.037)
PC1	0.14 (0.27)AB	1.15 (0.34)A	−1.05 (0.25)C	−0.42 (0.32)BC	8.54 (0.000)
PC2	−0.15 (0.19)	0.02 (0.26)	−0.12 (0.23)	0.53 (0.19)	1.45 (0.235)

TABLE 3. Factor loadings, eigenvalues, and proportion of the variance explained by the first 3 axes from the principal component analysis of nest placement variables for natural and used artificial nests of Eastern Kingbirds breeding at Malheur National Wildlife Refuge, Oregon, USA (2010–2011).

Variable	PC1	PC2	PC3
Nest angle (°)	0.466	0.381	0.058
Nest height (m)	0.466	−0.002	0.254
Distance of nest to top (m)	−0.510	0.113	0.006
Distance to canopy edge (m)	−0.272	0.661	−0.491
Distance to center of tree (m)	−0.450	−0.343	0.318
Nest cover (%)	0.173	−0.536	−0.767
Eigenvalue	2.498	1.104	0.929
Explained variance (%)	41.6	18.4	15.5
Σ Explained variance (%)	41.6	60.0	75.5

vertically oriented branch that was close to the center of the tree. PC1 scores of successful NATs exceeded those of both categories of ARTs, but PC1 scores of failed NATs and successful ARTs were similar (Table 2). Successful NATs had higher scores on PC1 than failed NATs ($t = 2.28$, $P = 0.03$), and the same pattern was evident in ARTs ($t = 1.58$, $P = 0.12$; Table 2). PC2 was a descriptor of variation in horizontal placement. Nests with high positive scores were located far from the canopy and close to the center of the tree and had little vegetative cover. No differences existed among failed and successful ARTs and NATs along PC2 on the basis of the ANOVA; but within ARTs, direct comparison by t-test showed that successful ARTs had higher scores than failed ARTs ($t = 2.02$, $P = 0.05$).

Fledging and Nest Success

Best-subsets regression ($n = 85$ nests) of fledging success yielded 3 informative models. The top model ($\Delta AIC_c = 0.0$) of angle of the nest branch and year was 1.68× more likely than the next-best model, which included angle of the nest branch, nest type (NAT vs. ART), and distance to the top of the tree ($\Delta AIC_c = 1.034$). The top model was 2.39× more likely than the third-best model of angle of the nest branch and nest type ($\Delta AIC_c = 1.743$). Angle of the nest branch had the highest importance weight (1.0), followed by nest type (0.504), year (0.496), and distance to the top (0.296). Model-averaged parameter estimates ($\pm$ SE) indicated that fledging success increased with nest branch angle ($\beta = 0.012 \pm 0.005$), was higher in 2011 ($\beta = 0.358 \pm 0.239$) and in ARTs ($\beta = 0.354 \pm 0.245$), but declined with increasing distance from the top of the tree ($\beta = -0.071 \pm 0.065$). Confidence intervals (CI) for nest type (−0.005 to 0.714) and distance to the top (−0.178 to 0.036) included zero, but those of angle of the nest branch (0.005 to 0.018) and year (0.008 to 0.708) did not. Hence, differences between years and in the angle of the nest branch contributed most to variation in fledging success.
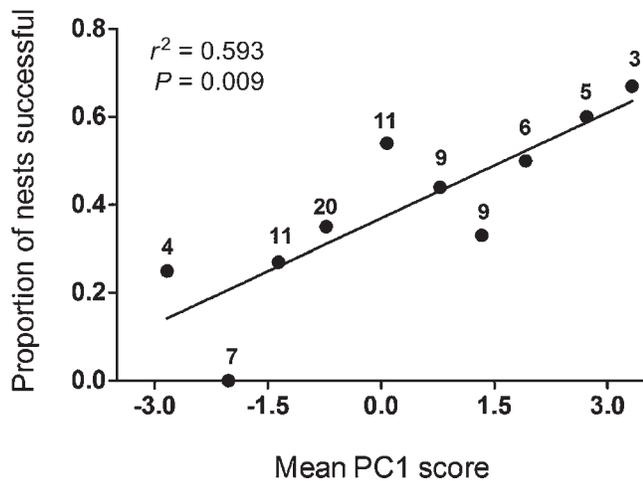
FIGURE 2. Average ($\pm$ SE) angle of the branch on which the nest was placed in relation to (**A**) average distance to the top of the tree and (**B**) average nest height of successful (NaSu) and failed (NaFa) natural Eastern Kingbird nests and of unused (ArUn), successful (ArSu), and failed (ArFa) artificial nests at Malheur National Wildlife Refuge, Oregon, USA (2010–2011).

tended to be on more vertically oriented branches, placed higher and closer to the top of the tree and closer to the center of the tree than their respective failed counterparts. By contrast, successful NATs and successful ARTs had the highest and lowest cover scores, respectively (Table 2). In general, locations of unused ARTs (Table 1) resembled those of failed NATs and successful ARTs and were least like successful NATs and failed ARTs (Table 2). On the basis of comparisons of nest branch angle and distance to the top of the tree, unused ARTs and failed NATs overlapped extensively (Figure 2A), but a plot of nest branch angle against nest height showed equally strong overlap between unused and successful ARTs (Figure 2B).

The PCA of nest variables yielded 2 useful axes. The first principal component (PC1) described vertical aspects of nest location (Table 3). Positive scores corresponded to nests located high in the tree and close to the top, on a

FIGURE 3. Proportion of nests to fledge young ("nest success") in relation to mean score on the first principal component (PC1) for natural and artificial nests that were binned into 10 evenly spaced bins at Malheur National Wildlife Refuge, Oregon, USA (2010–2011). Numbers above points represent sample sizes. The coefficient of determination (r^2) from the regression of nest success in relation to mean PC1 score was weighted by sample size, such that less weight was given to extreme low and high mean PC1 scores that had low sample sizes.

The importance of nest branch angle to fledging success (variation in which was due almost solely to nest predation) was not immediately apparent, because nest branch angle would seem more likely to affect nest stability and the likelihood of the nest falling or being blown from the tree by wind rather than it being discovered by a predator. Nest branch angle was an important contributor to PC1 (Table 3), and therefore we examined success in relation to position on PC1 by binning nests into 10 equal-sized bins and regressing nest success (proportion of nests in a bin to fledge ≥ 1 young) against mean PC1 score for nests included in each bin. We performed the same analysis for nest branch angle. Because of small sample sizes for bins at the low and high end, regression of proportion of successful nests against both mean PC1 score and mean nest branch angle of each bin were weighted by the bin's sample size. Proportion of successful nests increased with both mean PC1 score (r^2 of least-squares weighted regression [LSWR] = 0.593, $P = 0.009$; Figure 3) and mean nest branch angle (r^2 of LSWR = 0.492, $P = 0.024$), but mean PC1 accounted for 20.5% more (0.593/0.492 × 100%) of the variation in proportion of nests to fledge young than mean nest branch angle.

Analysis of variation in fledging success of successful nests yielded 2 models. The top model included nest cover, year, and nest type ($\Delta AIC_c = 0.0$) and was 1.37× more likely than the next-best model of nest cover and year ($\Delta AIC_c = 0.631$). However, model-averaged parameter estimates indicated that the CI for nest type included zero

($\beta = 0.396 \pm 0.277$, CI: -0.009 to 0.801). By contrast, confidence intervals for nest cover ($\beta = 0.237 \pm 0.090$, CI: 0.105 to 0.368) and year did not include zero ($\beta = 1.090 \pm 0.385$, CI: 0.526 to 1.654). Fledging success increased equally with nest cover in both years (equality of slopes: $F_{1, 27} = 0.65$, $P = 0.423$), but at any given level of cover, success was higher in 2011 (equality of elevation: $F_{1, 28} = 11.01$, $P = 0.002$).

DISCUSSION

Frequent use of artificial nests by kingbirds at our study site (Cancellieri and Murphy 2013) made it possible for us to take a novel approach to evaluate whether kingbirds actively choose nest sites and to assess the value of their choices. However, our data are limited because flooding in both years prevented us from distributing ARTs over the full range of potential nest sites and from measuring nest height from the true base of the tree. Both have the potential to influence the interpretation of our results. For instance, the low nest height at MNWR compared with other locations (see above) was partly an artifact of measuring height from the river bank. However, it also reflects the penchant that kingbirds have for nesting on lower, more horizontal branches in riparian and lacustrine habitats (Davis 1941, Blancher and Robertson 1985). An additional concern is the relatively small area over which nest cover was measured. We chose an area on the basis of our experience searching for nests and prior descriptions of nest conspicuousness that focused on this small area. Our measurements confirmed that little cover existed in the immediate area around the nest. However, vegetative cover 1–2 m above the nest might be important for obscuring the nest from avian predators searching overhead. Our failure to measure overhead cover leaves open the possibility that cover may still be important for nest success (but see below).

Assuming that nest-site selection is nonrandom, we expected the features of used and unused ART nest locations to differ. Active choice was indicated by the failure to use all 10 nests located over land. Among all remaining nests, we found that used ARTs were located farther from the top and center of the nest tree than unused ARTs, again suggesting active choice. Kingbird use of the other 4 variables did not differ, perhaps because of our inability to distribute nests across the full range of potential nest sites.

We also predicted that nest-site characteristics of used ARTs would be more similar to NATs than were unused ARTs, but we instead found that unused ARTs were in locations that tended to more closely match sites where NATs were located (Figure 1). We suggest that this paradoxical finding exists for 2 reasons. First, kingbirds appear to prefer sites either well up in trees on vertically

oriented branches (MacKenzie and Sealy 1981, Murphy 1983) or much lower, on relatively horizontal branches, especially when they nest over water (Davis 1941, Blancher and Robertson 1985). We positioned few ARTs at the highest points in trees and instead placed most ARTs in intermediate to lower positions that we could reach. If kingbirds indeed prefer extreme vertical or horizontal locations, then ARTs placed in intermediate positions would go unused but more closely resemble locations of NATs than would used ARTs. However, this argument is only tenable if few NATs were located lower on relatively horizontal limbs, and this leads to the second explanation. Many ARTs were located lower in the trees and over water, and these were heavily represented in the used ART category. Most females with ARTs in their territory used them (76%; Cancellieri and Murphy 2013). Thus, the difference in height and vertical orientation of NATs and used ARTs is exaggerated because most females that would have built nests at lower heights used ARTs instead of constructing their own nests. Females gained no apparent advantage from using the ARTs (Cancellieri and Murphy 2013), so presumably they used them because they provided a good substrate in a frequently used nesting location.

Breeding Success and Nest Location

As in most open-cup–nesting birds (Ricklefs 1969, Martin 1993), nest success averaged <50% over the 2 yr and nest predation accounted for nearly all (>90%) nest losses in both years. Some have argued that adaptive nest-site choice is impossible when such intense predator pressure reduces the probability of success to little more than a stochastic event (Filliater et al. 1994). Indeed, most published studies fail to show that the most commonly used sites are more likely to produce young (reviewed by Chalfoun and Schmidt 2012). However, prior work on kingbirds (Murphy 1983) and other species (Martin and Roper 1988, Wilson and Cooper 1998, Siepielski et al. 2001, Peluc et al. 2008) provide counterexamples. Moreover, some species modify nest placement in response to negative past experiences (Marzluff 1988, Forstmeier and Weiss 2004) or perceived predation risk (Peluc et al. 2008, Zanette et al. 2011, Latif et al. 2012). This strongly supports the view that nest-site choice is flexible and adaptive.

For NATs, successful nests were placed on more upwardly angled branches that were closer to the top of the tree than failed nests. Successful NATs also had higher PC1 scores, which follows from this axis's association with nest branch angle and vertical aspects of nest placement (Table 3). Direct comparisons of successful and failed ARTs (by *t*-tests) suggested strong tendencies for successful ARTs to be placed higher and closer to the center of the nest tree than failed ARTs. The same pattern, albeit nonsignificant, existed among NATs. As in NATs, nest branch angle of successful ARTs was more than twofold steeper than that of failed ARTs. Thus, parallel associations existed between placement and success in both nest types. Successful NATs and ARTs were located higher in the tree and closer to the tree's center on more upwardly angled branches, which is fully consistent with the increase in the proportion of nests to fledge young along PC1 (Figure 3). The stronger association of mean nesting success with PC1 than with nest branch angle suggests that nest branch angle is not, in and of itself, the factor influencing success. Rather, it is no doubt one of a set of correlated traits represented by PC1 that strongly influences the probability of success. The positive association of kingbird nest success with the major gradient describing nest placement (PC1), and the consistency in the patterns shown by NATs and ARTs, supports our prediction that kingbird nest success is site dependent and would depend on locating the nest in defensible sites higher in trees, and that nest cover would little influence the probability that a nest would fledge young (also see Weidinger [2002] for European thrushes).

However, greater nest cover was associated with higher fledging success when analyses were restricted to successful nests. As noted by others (see comments in Bent 1942) and quantified by us (Table 2), kingbird nests are often exposed and visually conspicuous (for similar comments on a congener, see Ricklefs 1977). Under these circumstances, nest cover likely has little effect on whether a predator locates a nest. Thus, nest cover's apparent irrelevance to the success of entire nests—yet contribution to the productivity of successful nests—is probably because nest predation is an all-or-nothing event in most species. Work at MNWR over the 8 yr prior to our study implicated magpies as primary nest predators, and although a kingbird pair can defend their nest against a single magpie (M. T. Murphy personal observation), they are hard pressed to drive family groups of 4–7 magpies from the vicinity of the nest once it has been discovered. Our failure to measure overhead cover for nests, although of concern for some predators (e.g., Common Ravens [*Corvus corax*] and *Accipiter* spp.), would not likely influence the probability of nest discovery by magpies because of the methodical searches made by family groups of magpies that move through foliage rather than fly above it (M. T. Murphy personal observation). Cover for nests that escaped predation may be important because of its potential to affect microclimate and physical stresses experienced by young. Kingbird nests are often exposed to sunlight, and the high temperatures and high insolation of midsummer may force females of nests with low nest cover to stay at the nest to shade young rather than forage for food. Thus, the principal value of nest cover is likely to

be found in its capacity to affect microclimate (e.g., Lloyd and Martin 2004).

We have shown that the likelihood of kingbird success, whether they used natural or experimentally supplied nests, varied along the primary axis describing nest placement. Nest-site choice and parental behaviors are inextricably linked (Ricklefs 1977), and many of the sites used by kingbirds would be unlikely to suit most species unless they possessed the kingbird's well-established nest-vigilance (Woodard and Murphy 1999) and nest-defense behaviors (Blancher and Robertson 1982, Siderius 1993, Redmond et al. 2009a). We suspect that our ability to detect a positive relationship between success and nest-site choice, which is often not the case (see review by Chalfoun and Schmidt 2012), is explained by the relatively depauperate predator community faced by kingbirds at MNWR. By nesting well above ground, and generally over water, kingbirds at MNWR greatly reduce threats of predation by many potential nest predators. Avian predators are the exception, and despite complementary nest-site choice and defense behavior, the en masse foraging of magpies takes a toll on kingbirds. Nonetheless, the reduction of the potential set of nest predators to mainly one species facilitates an adaptive response to threats of nest predation and enabled its quantification by us.

The result most difficult to reconcile with a model of adaptive nest-site selection is the overlap in locations of failed NATs and unused and successful ARTs (Figure 2). Similarity in placement of failed NATs and unused ARTs was predicted, but overlap of both with successful ARTs, especially failed NATs and successful ARTs, is inconsistent with an adaptive choice model. Overlap may be attributable to a lack of consideration of appropriate temporal and spatial scales in our analyses. For instance, nest-site use may be dependent on age (Pinkowski 1979) or contingent on past experience with particular nest locations in a tree (Marzluff 1988, Hauber 2001) or previous nest failure by an individual at a particular territory (Murphy 1996b, Hoover 2003). Moreover, knowledge of conspecific reproductive success substantially influences habitat use in some species (Ward 2005, Redmond et al. 2009b). All may cause otherwise high-quality nest sites to go unused or lead to use of less-than-ideal sites. Variation in nest success is also often best understood from a hierarchical multiscale perspective that includes nest sites, habitat surrounding the nest, and the larger landscape (Hatchwell et al. 1996, Clark and Shutler 1999, Misenhelter and Rotenberry 2000, Citta and Lindberg 2007). The pairs that we studied all nested within the same landscape, but the proportion of the riverbank covered by willows in the 40 m surrounding each NAT and ART varied nearly tenfold (12–100%; M. T. Murphy personal observation). The extent to which characteristics of the "habitat patch" affected use of a particular ART or influenced nest success of both nest types is unknown but may help explain overlap in placement of failed NATs and unused or successful ARTs. Thus, while our experimental approach added a new element to attempts to understand nest-site selection by birds, overlap in the sites of failed NATs and unused and successful ARTs highlights the difficulty of accounting for all contingencies. Future work, in this and other systems, should strive to account for individual histories of birds and utilize designs that incorporate a larger spatial context to ensure continued progress in our attempts to understand avian nest-site choice.

ACKNOWLEDGMENTS

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